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HYBRIDIZATION IN THE BABASSU PALM COMPLEX: I. ORBIGNYA PHALERATA × O. EICHLERI[1,2]

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ABSTRACT

The babassu palm (*Orbignya phalerata*) is an important source of oil and charcoal in Brazil. In some areas it grows in association with *O. eichleri,* and where their distribution is sympatric, a third palm is found. This taxon was described by Bondar in 1954 as *O. teixeirana.* As a result of intense fieldwork and subsequent morphological and anatomical studies, we conclude that *O. teixeirana* is a hybrid between *O. phalerata* and *O. eichleri* and propose a change in its status to reflect this new understanding of its origin.

MANY PALMS have long been poorly understood taxonomically. The frequently large sizes of their stems, leaves and inflorescences have impeded proper collections, with the result that critical parts of genera and species are underrepresented in herbaria (Balick, Anderson and da Silva, 1982). Earlier in this century many new species were distinguished on the basis of quantitative morphological differences found on a limited number of specimens. More intensive collections in recent years have enabled taxonomists to appreciate the high degree of phenotypic plasticity in some characters formerly considered to be constant. Concomitant with this recognition is a realization that palms of some groups may frequently hybridize. Studies by Glassman in *Syagrus* (1968, 1970, 1971), Wessels Boer in *Bactris* (1971) and Dahlgren and Glassman in *Copernicia* (1963) have documented numerous new hybrids in palms, primarily in the Cocoeae. (For a definition of this group, see Dransfield and Uhl, 1986.)

Bondar (1954) described *Orbignya teixeirana* from a specimen he collected near the town of Caxias, in the Brazilian state of Maranhão. He presented a key that distinguished this new species from the widespread and common "babaçu" palm (spelled "babassu" in English), which he recognized as *O. speciosa* (Mart.) Barb. Rodr., and the acaulescent palm known as "piaçava" (spelled "piassava" in English), *O. eichleri* Drude. Bondar provided a brief description of the new species, as well as photographs of its inflorescence and fruit. In his description, Bondar wrote that *O. teixeirana,* known locally as "perinão," was found in the localities where babassu and piassava were also present, and was "probably a hybrid of the two." Despite his suspicion of the hybrid status of the perinão palm, Bondar described it as a new species. The types were reported to have been deposited in the Rio de Janeiro Botanical Garden (RB) and the Field Museum of Natural History (F), although no collection

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numbers or specific collecting locality were provided. According to Glassman (1977), the holotype is Bondar s.n. (RB-80813), and an additional collection is also found at the Field Museum of Natural History (F-405257). Bondar dedicated this species to Dr. Edgard Teixeira Leite in gratitude for his support of Bondar's studies.

In 1980 we began to investigate the genus *Orbignya* as part of a program to domesticate the babassu palm, which is widely used in Brazil as a source of oil and charcoal. In the Brazilian state of Maranhão alone over one million people collect babassu fruits and crack them to extract the oil-rich kernels for subsistence and market production of vegetable oil; the remaining woody endocarp provides the region's most important source of domestic fuel in the form of charcoal. Extraction of babassu kernels comprises the largest oilseed industry in the world entirely dependent on a wild plant for its raw material, with an annual cash value of over US $100,000,000 in oil produced (Pick et al., 1985). While collecting germplasm of these palms, we gathered extensive data on their ecology, ethnobotany, and taxonomy.

To determine the status of *Orbignya teixeirana,* we first had to resolve the taxonomy and nomenclature of its suspected parents: babassu and piassava. The taxonomic status of babassu, as well as its proper nomenclature, has been a prolonged topic of debate among botanists, and this debate has even spilled outside of the botanical community. For example, the Brazilian National Economic Council and the Association of Commerce in Maranhão took a stand on nomenclature, adopting *O. speciosa* as the official name of the babassu palm (Markley, 1971).

A detailed discussion of the taxonomic status and nomenclature of babassu is provided by Anderson and Balick (in press). They conclude that this complex is comprised of two distinct species. The most widespread and economically important is *Orbignya phalerata* Mart.; the second species, *O. oleifera* Burret, is apparently confined to the São Francisco river valley in Minas Gerais (with possible outlying populations in adjacent areas of Goiás and Bahia). Adoption of *O. phalerata* as the name for the predominant species in the babassu complex resolves nearly a century of nomenclatural debate. The palm referred to by Bondar (1954) as *O. speciosa* is now reduced to synonymy under *O. phalerata.* The original scientific name for the piassava palm, *O. eichleri* Drude, remains in good standing (Glassman, 1977).

This study describes the morphology and leaf anatomy in three taxa of *Orbignya*: babassu, perinão, and piassava. To date, the only published information on leaf anatomy in *Orbignya* (Tomlinson, 1961) is confined to the generic level. Determining the status of purported hybrids in palms has invariably been based on morphology, and this study represents the first such attempt that, to our knowledge, uses both anatomical and morphological comparisons. Tomlinson (1961) considered that palms cannot normally be distinguished at the specific level through the use of anatomical leaf characters. However, he believed that the latter were of value in systematic classification when combined with other lines of evidence such as morphology. Various workers have since used leaf anatomy coupled with morphological evidence to assist in distinguishing palms at the specific level (e.g., Glassman, 1972: *Syagrus*; Uhl, 1972: *Chelyocarpus* alliance; Read, 1975: *Thrinax*; Uhl, 1978: *Hyophorbe*).

MATERIALS AND METHODS—*Morphological studies*—Due to the lack of adequate herbarium specimens of *Orbignya,* we initiated an intensive field collecting program in 1980. Obtaining specimens of large palms, such as many of the species in this genus, requires a highly specific collecting methodology, the details of which are provided by Balick et al. (1982). Because it is often not possible to obtain a complete representation of each morphological component, collecting must be selective and accompanied by detailed field documentation.

Our overall collecting stategy was to obtain as wide a representation as possible of the variability within the species comprising the babassu complex. Specimens of *Orbignya phalerata* were obtained over widespread areas in Brazil and Bolivia (Fig. 1). Specimens of the purported hybrid described in this paper, as well as *O. eichleri,* were obtained at a total of four locations in Brazil, three in the state of Maranhão and one in the state of Goiás (Fig. 1). At each of these locales, we made repeated collections of the purported hybrid so as to obtain a better representation of its variability. Specimens were distributed among herbaria in Brazil (CEN, IAN, INPA, MG), Bolivia (LPB), and the United States (NY).

Detailed studies of the morphology and anatomy of these palms were carried out at the Lieberman Laboratory and Institute of Economic Botany of the New York Botanical Garden. Morphological comparisons were made over the full range of characters, from those apparent in the field to those only discernible in the laboratory. For quantitative compari-

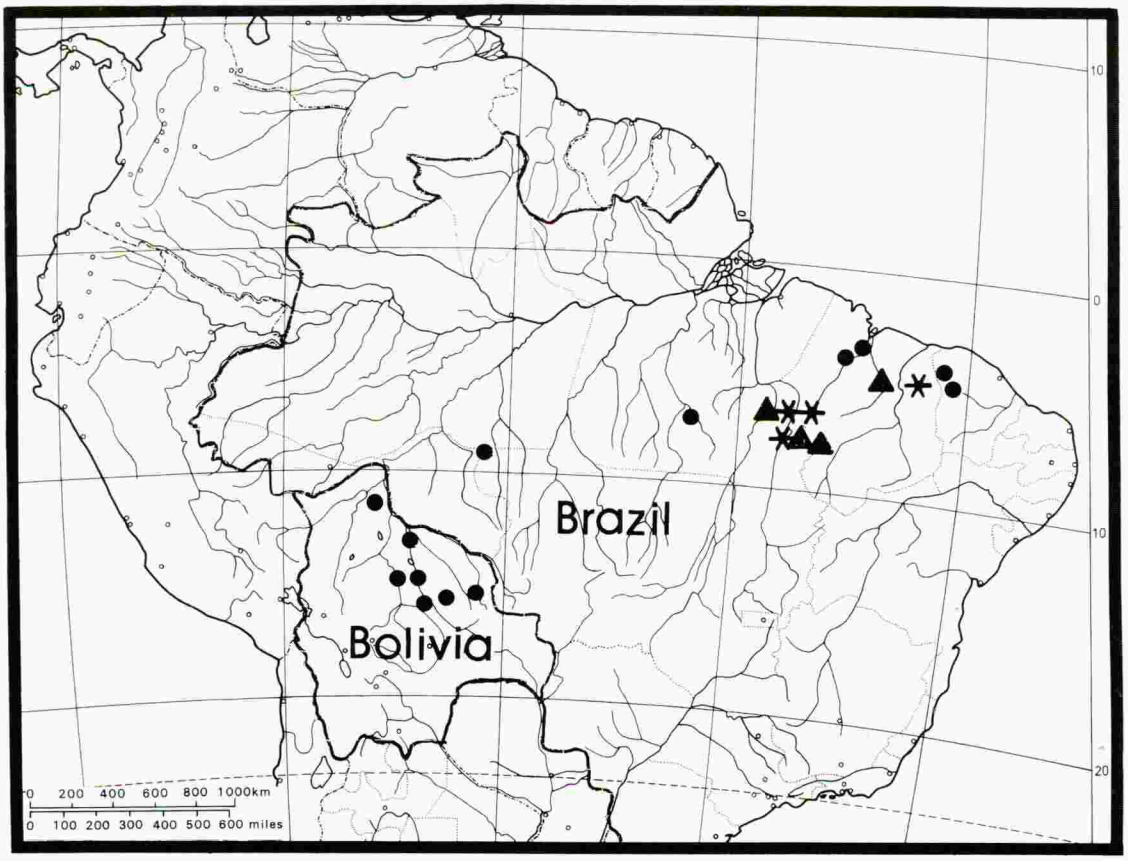


Fig. 1. Collections of the hybrid complex made for this study: circles = *Orbignya phalerata*; stars = *O. eichleri*; triangles = *O.* ×*teixeirana*.

sons, repeated measurements from numerous specimens were obtained, and the mean as well as the range of these measurements was usually determined, except in cases where the sample sizes were judged to be too small.

Anatomical studies—For each of the three taxa, three collections considered to be representative were selected for anatomical studies. The material used in the preparation of anatomical sections was removed from the pinnae along the middle of the leaf and treated according to the methodology described by Martens and Uhl (1984) for the preparation of palm leaf cross-sections. Each of the sections comprised the entire width of the pinna, including the midrib. It was quite difficult to make these sections due to the presence of silica bodies and fibers, as well as the large size of the leaves. Preparation of the material included fixing, desilification, initial softening and dehydration. Each pinna was embedded in Paraplast Plus and cut with an A. O. Spencer 820 Rotary Microtome in 15 micron sections. Safranin and Fast Green were used as stains. It was discovered that best staining results were obtained by keeping the slides immersed five hours in the Safranin and 25–30 seconds in the Fast Green stains. Epidermal peels were made using the techniques described by O'Brien and McCully (1981). To make the peels, pinnae were removed, hydrated, cut in samples ca. 2 × 3 cm, mascerated and stained in Safranin. To analyze venation patterns in the leaves, pinnae samples were bleached and then stained in Safranin, according to the technique described by Martens and Uhl (1984).

RESULTS—Morphological and anatomical descriptions of the three taxa are provided below. To facilitate comparison, synopses of distinguishing morphological and anatomical characters are given in Tables 1 and 2, respectively.

Morphological descriptions (Fig. 2–5)

Orbignya phalerata Mart., Palm. Orbig. 126, t. 13, fig. 2, 32A. 1884. Type: d'Orbigny 20 (P, n.v.).

TABLE 1. *Morphological comparison of* Orbignya phalerata *Mart.,* O. ×teixeirana *(Bondar) Balick, Pinheiro and Anderson, and* O. eichleri *Drude. Values indicate ranges; means in parentheses, except when sample size is too small*

Character	*O. phalerata*	*O. ×teixeirana*	*O. eichleri*
STEM			
Length in adults (m)	5.0–30.0 ($\bar{x}$ = 11.5)	0.5–7.1 ($\bar{x}$ = 4.3)	0
DBH (cm)	19–50 ($\bar{x}$ = 38)	19–25 ($\bar{x}$ = 2)	0
LEAF			
Number per palm	10–25 ($\bar{x}$ = 15)	10–13 ($\bar{x}$ = 11)	3–8 ($\bar{x}$ = 4)
Sheath:			
Length in adults (cm)	40–120 ($\bar{x}$ = 98)	40–90 ($\bar{x}$ = 54)	20–33 ($\bar{x}$ = 27)
Maximum width (cm)	21–42 ($\bar{x}$ = 32)	15–30 ($\bar{x}$ = 21)	1.8–3.0 ($\bar{x}$ = 2.2)
Striations on abaxial surface	Generally present	Present or absent	Absent
Petiole:			
Length in adults (cm)	8–42 ($\bar{x}$ = 24)	21–80 ($\bar{x}$ = 46)	30–80 ($\bar{x}$ = 53)
Maximum width (cm)	5–30 ($\bar{x}$ = 18)	3–8 ($\bar{x}$ = 5)	1.5–2.3 ($\bar{x}$ = 1.8)
Rachis:			
Length in adults (m)	5.6–8.6 ($\bar{x}$ = 7.5)	2.0–6.4 ($\bar{x}$ = 3.7)	1.2–2.1 ($\bar{x}$ = 1.6)
Cross section	4-Sided	Usually 4-sided, rarely triangular	Usually triangular, rarely 4-sided
Abaxial surface	Weakly to strongly lepidote	Smooth to moderately lepidote	Smooth
Pinnae:			
Number per side	156–208 ($\bar{x}$ = 196)	104–153 ($\bar{x}$ = 130)	76–89 ($\bar{x}$ = 84)
Orientation	In same plane	In same plane to crispate	Crispate
Arrangement	Regular	Clustered to regular	Clustered
Adaxial surface	Dull to lustrous	Dull	Dull
Abaxial surface	Weakly glaucous	Weakly glaucous to smooth	Mostly smooth
Length × width (cm)			
Basal pinna	83–185 ($\bar{x}$ = 135) × 1.0–2.0 ($\bar{x}$ = 1.5)	40–185 ($\bar{x}$ = 95) × 0.5–2.5 ($\bar{x}$ = 1.0)	45–70 ($\bar{x}$ = 55) × 0.7–1.5 ($\bar{x}$ = 0.9)
Middle pinna	88–168 ($\bar{x}$ = 116) × 2.0–6.0 ($\bar{x}$ = 4.4)	53–112 ($\bar{x}$ = 85) × 2.2–4.0 ($\bar{x}$ = 3.0)	37–81 ($\bar{x}$ = 55) × 1.4–3.0 ($\bar{x}$ = 2.1)
Apical pinna	22–139 ($\bar{x}$ = 52) × 0.8–2.3 ($\bar{x}$ = 1.6)	14–33 ($\bar{x}$ = 26) × 0.2–15 ($\bar{x}$ = 1.7)	14–42 ($\bar{x}$ = 21) × 0.2–0.8 ($\bar{x}$ = 0.4)
INFLORESCENCE			
Bracts:			
Length of prophyll (cm)	50–150	30–33	ca. 20
Length of peduncular bract (cm)	40–218 ($\bar{x}$ = 154)	85–130 ($\bar{x}$ = 113)	35–65 ($\bar{x}$ = 46)
Length of acumen (cm)	16–40 ($\bar{x}$ = 27)	3–20 ($\bar{x}$ = 16)	3–12 ($\bar{x}$ = 7)
Abaxial surface of peduncular bract	Tan to rust brown	Rust brown to blood red	Rust brown to blood red

TABLE 1. *Continued*

Character	*O. phalerata*	*O. ×teixeirana*	*O. eichleri*
Primary Axis:			
Length of peduncle (cm)	56–185 ($\bar{x}$ = 106)	44–88 ($\bar{x}$ = 73)	5–37 ($\bar{x}$ = 18)
Length of rachis (cm)	48–175 ($\bar{x}$ = 97)	34–99 ($\bar{x}$ = 66)	17–35 ($\bar{x}$ = 24)
Curvature	Not curved	Weakly to strongly curved	Strongly curved
Rachillae:			
Number on staminate inflorescence	277–401 ($\bar{x}$ = 339)	41–150 ($\bar{x}$ = 84)	15–35 ($\bar{x}$ = 23)
Number on androgynous inflorescence	323–475 ($\bar{x}$ = 400)	20–70 ($\bar{x}$ = 46)	10–20 ($\bar{x}$ = 12)
Length on staminate inflorescence (cm)	18–28 ($\bar{x}$ = 23)	1–20 ($\bar{x}$ = 11)	2.3–15 ($\bar{x}$ = 7.6)
Length on androgynous inflorescence (cm)	10–24 ($\bar{x}$ = 16)	0.1–2.9 ($\bar{x}$ = 1.0)	0.1–1.0 ($\bar{x}$ = 0.4)
Disposition on rachis	Throughout	On abaxial side	On abaxial side
Length of subtending bracteole on staminate inflorescence (mm)	0.5–6.0 ($\bar{x}$ = 3.2)	0.5–7.5 ($\bar{x}$ = 2.5)	1.0–4.0 ($\bar{x}$ = 1.6)
Length of subtending bracteole on androgynous inflorescence (mm)	2.0–14.0 ($\bar{x}$ = 5.9)	0.5–30.0 ($\bar{x}$ = 8.5)	3.0–45.0 ($\bar{x}$ = 14.4)
STAMINATE FLOWER			
Sepals:			
Number per flower	3–4 ($\bar{x}$ = 3.1)	3 ($\bar{x}$ = 3)	2–4 ($\bar{x}$ = 3)
Length (mm)	0.8–2.5 ($\bar{x}$ = 1.3)	0.6–1.6 ($\bar{x}$ = 1.1)	0.4–4.9 ($\bar{x}$ = 1.1)
Width (mm)	0.6–2.3 ($\bar{x}$ = 1.1)	0.6–1.3 ($\bar{x}$ = 0.9)	0.5–2.0 ($\bar{x}$ = 1.0)
Consistency	Coriaceous	Membranous to coriaceous	Membranous to coriaceous
Petals:			
Number per flower	2–3 ($\bar{x}$ = 2.1)	1–2 ($\bar{x}$ = 1.6)	1–4 ($\bar{x}$ = 1.4)
Length (mm)	9.5–16.9 ($\bar{x}$ = 13.0)	7.0–11.8 ($\bar{x}$ = 9.3)	6.2–12.4 ($\bar{x}$ = 9.2)
Width (mm)	2.8–7.5 ($\bar{x}$ = 4.3)	3.0–9.0 ($\bar{x}$ = 5.6)	1.5–11.6 ($\bar{x}$ = 6.8)
Consistency	Coriaceous	Membranous to coriaceous	Membranous to fibrous
Stamens:			
Number per flower	21–30 ($\bar{x}$ = 25)	18–26 ($\bar{x}$ = 22)	14–20 ($\bar{x}$ = 17)
Anther shape	Irregular	Irregular, semi-elongated	Irregular, elongated
Fusion of thecae	Separate	Separate or united	United
PISTILLATE FLOWER			
Number of bracteoles per flower	3	2–4	1–3
Sepals:			
Number per flower	3–6	3	3
Length (cm)	2.8–4.1	2.4–3.5	1.9–3.5
Shape	Triangular to deltate	Triangular to deltate	Triangular

TABLE 1. *Continued*

Character	*O. phalerata*	*O.* × *teixeirana*	*O. eichleri*
Petals:			
Number per flower	3–5	3–4	3–6
Length (cm)	2.3–5.0	2.2–3.4	1.3–2.8
Margins	Dentate	Smooth	Smooth to slightly dentate
FRUIT			
Length (cm)	6.6–12.5 ($\bar{x}$ = 9.7)	5.4–9.1 ($\bar{x}$ = 7.9)	4.8–7.7 ($\bar{x}$ = 5.9)
Width (cm)	3.7–9.9 ($\bar{x}$ = 6.3)	3.4–5.9 ($\bar{x}$ = 5.1)	3.3–4.4 ($\bar{x}$ = 4.2)
Dry weight (gm)	40–480 ($\bar{x}$ = 176)	18–210 ($\bar{x}$ = 82)	10–50 ($\bar{x}$ = 22)
Height of calyx cupule (cm)	3.8–5.8 ($\bar{x}$ = 4.8)	3.4–5.9 ($\bar{x}$ = 4.2)	3.3–4.9 ($\bar{x}$ = 3.7)
Staminodal ring	Weakly to strongly defined	Weakly to moderately defined	Weakly defined
Number of seeds	1–11	5–7	4–7

Attalea speciosa Mart., Hist. Nat. Palm 2: 138, t. 96, fig. 3–6. 1826. Type: Martius s.n. (M, n.v.). *Orbignya speciosa* (Mart.) Barb. Rodr., Sert. Palm. Bras. 1: t. 52–53.

Orbignya martiana Barb. Rodr., Palm. Mattogross. 68, t. 22–23, fig. 1–14. 1898. Type: t. 22–23.

Orbignya macropetala Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 690. 1932. Type: Schomburgk s.n. (B?, n.v.).

Orbignya barbosiana Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 690. 1932. Type: published as a new name for *O. speciosa* (Mart.) Barb. Rodr.

Large, solitary, erect, pleonanthic, sometimes monoecious but commonly androdioecious, palm; stem columnar, frequently massive, 5–30 m high, 19–50 cm in diameter, surface gray to brown, smooth, obscurely ringed with leaf scars, adventitious roots sometimes visible at base.

Leaves 10–25, fewer in young or senescent plants, spirally arranged in a suberect (when young) or erect-arching (when mature) crown; sheath 40–120 cm long, 21–42 cm wide, partially clasping, split opposite the petiole, thick, coriaceous, abaxial surface green, weakly white lepidote, usually with yellow, longitudinal striations that may extend to the rachis, adaxial surface brown; petiole 8–42 cm long, 5–30 cm wide, green, smooth, channeled adaxially, convex abaxially; rachis 5.6–8.6 m long, base trough-shaped in cross section, more or less 4-sided at center, becoming triangular toward apex, abaxial surface weakly to strongly orange-brown lepidote, vestiture especially apparent when young, becoming gray with age and falling away; pinnae 156–208 per side, regularly inserted along the rachis and in a single plane, rigid when young, becoming pliant with age, linear-lanceolate at center of rachis, plicate, acute, basally reflexed at attachment, 1-ribbed with prominent intermediate veins, glossy dark green and smooth adaxially, dull-glaucous abaxially, basal pinnae 83–185 cm long and 1.0–2.0 cm wide, middle pinnae 88–168 cm long and 2.0–6.0 cm wide, apical pinnae 22–139 cm long and 0.8–2.3 cm wide.

Inflorescences interfoliar, cream-white in bud, yellow at anthesis, finally turning greenish to brown, branched to 1 order, bearing a pliable, fibrous prophyll 50–150 cm long (usually disintegrating rapidly upon development of the inflorescence); peduncular bract 40–218 cm long, woody, longitudinally strongly-ribbed, brown, swollen in middle, opening lengthwise, persistent, with acumen 16–40 cm long, interior surface of bract white-to-yellow lepidote at anthesis, becoming tan to rust-brown over

TABLE 2. *Selective comparison of anatomical characters in leaves of* Orbignya phalerata *Mart.*, O. ×teixeirana *(Bondar) Balick, Pinheiro and Anderson and* O. eichleri *Drude*

Character	*O. phalerata*	*"O. ×teixeirana"*	*O. eichleri*
Abaxial hypodermis	2 Layers	Generally 1 layer but occasionally 2 layers	1 Layer
Adaxial fibers	Small strands or rows, scattered	Intermediate-sized strands or rows, moderately concentrated	Large strands without rows, heavily concentrated
Inner sheath of primary and secondary veins	Fibers completely surrounding veins	Fibers incompletely surrounding veins, lacking on adaxial side	Fibers incompletely surrounding veins, lacking on adaxial side
Buttresses	Absent	Rare	Usually present

time; peduncle 56–180 cm long, elliptic to ovate in cross-section: rachis 48–175 cm long; rachillae of staminate inflorescence simple, 277–401 in number, 18–28 cm long, linear to slightly undulate, slender, attenuate, arranged spirally along the rachis, each rachilla subtended by a bract 0.5–6.0 mm long, bearing 17–102 staminate flowers arranged in 2(4) longitudinal rows on the abaxial side only; rachillae of androgynous inflorescence 323–475 in number, 10–24 cm long, linear to undulate, slightly thicker than rachillae on staminate inflorescences, arranged spirally along the rachis, each rachilla subtended by a bract 2.0–14.0 mm long and bearing 1–2(3) pistillate flowers at base to middle and 1–several usually inviable staminate flowers at apex, or sometimes bearing staminate flowers only.

Flowers unisexual; staminate flowers yellowish, slightly fragrant, asymmetrical, subtended by 2 small bracteoles per flower, 1.0–4.0 mm long; sepals 3, free or basally connate, lanceolate to triangular, 0.8–2.5 mm long and 0.6–2.3 mm wide, coriaceous; petals 2(3), free, incurved, occasionally imbricate along the margins or apex, more or less similar in length but always with 1 petal wider than the other(s), the wider petal 9.6–16.8 mm long and 3.9–7.5 mm wide, obovate, dentate at apex, the narrower petal(s) 9.5–16.9 mm long and 2.8–5.2 mm wide, narrowly elliptic, acute or occasionally dentate at apex, all petals coriaceous with smooth margins; stamens free, (21–)24–26(–30); filaments slender, linear to slightly narrowed toward apex, straight to occasionally slightly undulate, 1.0–4.2 mm long, infrequently fused; anthers irregularly shaped, spirally twisted, thecae united, irregularly coiled and twisted, longitudinally dehiscent; pollen grains free; pistillode much reduced.

Pistillate flowers cream-yellow, partially covered with a rust-colored tomentum, bracteolate; sepals 3–6, free, imbricate, 2.8–4.1 cm long at anthesis, variably shaped but generally triangular, hooded-concave, margins smooth, inner sepals coriaceous; petals 3(4–5), free, imbricate, 2.3–5.0 cm long at anthesis, variably shaped but generally triangular to deltate, hooded-concave, coriaceous, margins dentate, apex acute or dentate with 2–3 teeth; staminodial cupule leaving a ring around the pistil; gynoecium syncarpous; ovary superior; carpels (1–)3–6(–11); stigmas (1–)3–6(–11), erect to more or less reflexed at anthesis.

Fruits broadly elliptic to oblong, 6.6–12.5 cm long, 3.7–9.9 cm wide, 40–480 g each (dry weight), lepidote, surface gray-white at apex, rust-brown beneath, apex delineated in mature fruits by a more or less distinct ring left by staminodial cupule; stigmatic residue persistent; a cupule of indurate perianth enclosing base of fruit, 3.8–5.8 cm long; epicarp 1.0–4.0 mm thick, fibrous; mesocarp 2.0–12.0 mm thick, mealy-dry at maturity; endocarp 35–76 mm in diameter, woody and very hard; seeds (1–)3–6(–11), ovate to elliptic, 3–6 cm long; endosperm white, oily, homogeneous; embryo cream-white.

Specimens examined—BOLIVIA. Dept. Beni: Prov. Marban, ca. 35 km S of Trinidad, 10 km S of Sachojere, Villa Alba, Jul 1982, *Balick et al. 1359* (LPB, NY); 30 km S of Riberalta, island in Lake Tumi-Chucua, 2 Aug 1982, *Balick et al. 1367* (LPB, NY); Prov. Mamoré, ca. 18 km S of San Joaquin, farm called "Barranquita," 18 Aug 1982, *Balick et al. 1432* (LPB, NY); Dept. Santa Cruz: Prov. Velasco, ca. 105 km N of San Ignácio and 22 km S of San Simon, near Finca Bonanza, 26 Jul 1983, *Hopkins et al. 112* (LPB, NY); Prov. Nuflo de Chaves, on road between Yotaú and Ascerado La Luna, 6 Aug 1983, *Hopkins et al. 158* (LPB, NY). BRAZIL. Estado do Ceará: Mun. Ubajara, halfway between the town of Ubajara and Ubajara National Park, Dec 1981, *Balick et al. 1353* (CEN, IAN, INPA, MG, NY); Mun. Ipú, on road between Ubajara (62 km) and Ipú (11 km), 12 Dec 1981, *Balick et al. 1354* (CEN, IAN, INPA, MG, NY). Estado de Goiás: Mun. Tocantinópolis, 11 km from Tocantinópolis on Fazenda Mucamba, 28 Nov 1981, *Balick*

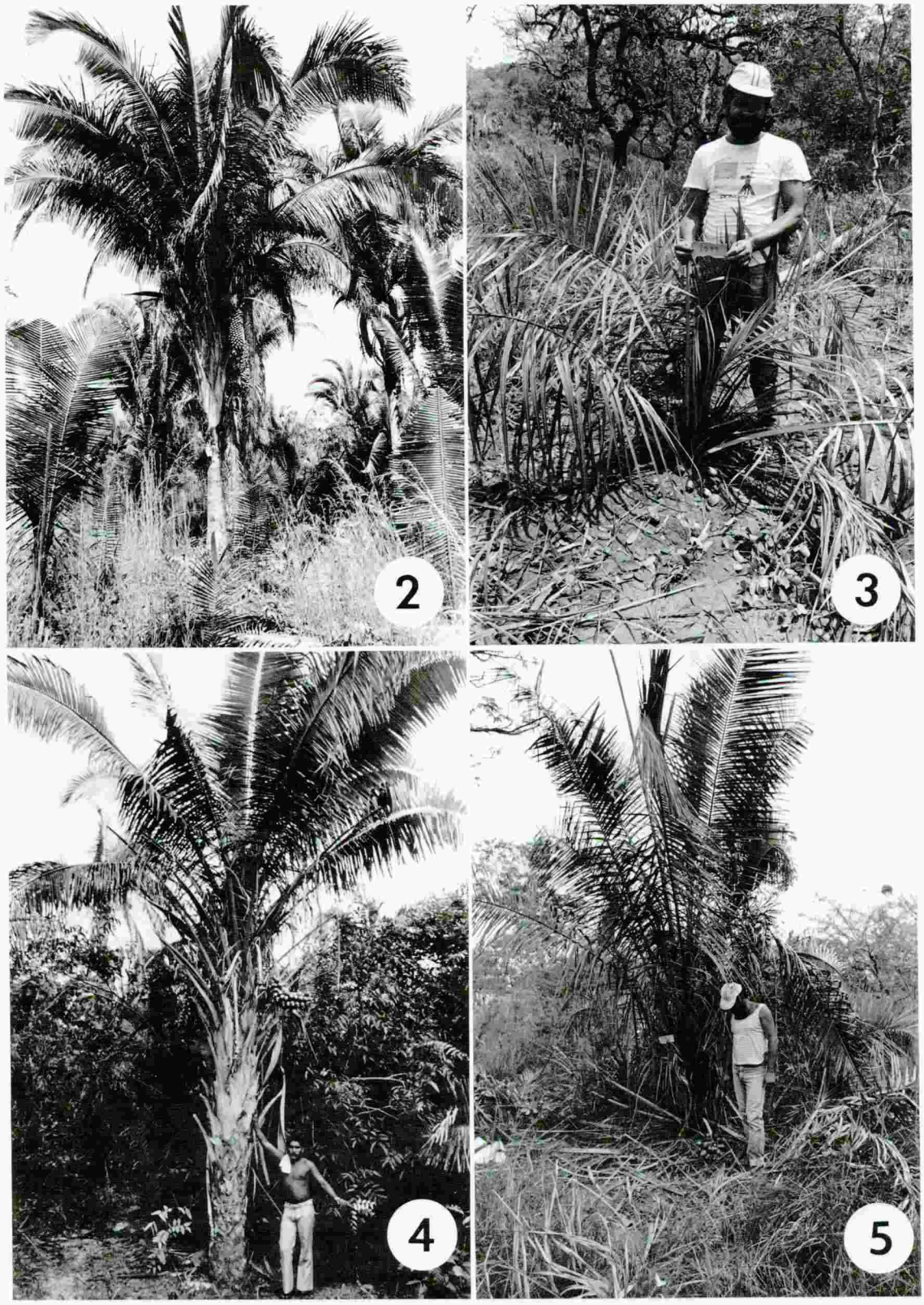


Fig. 2–5. **2.** *Orbignya phalerata* (uncollected population in Maranhão). **3.** *O. eichleri* (Balick et al. 1597). **4.** *O.* ×*teixeirana* with well-developed trunk (Anderson 395). **5.** *O.* ×*teixeirana* showing acaulescent habit (Balick et al. 1604).

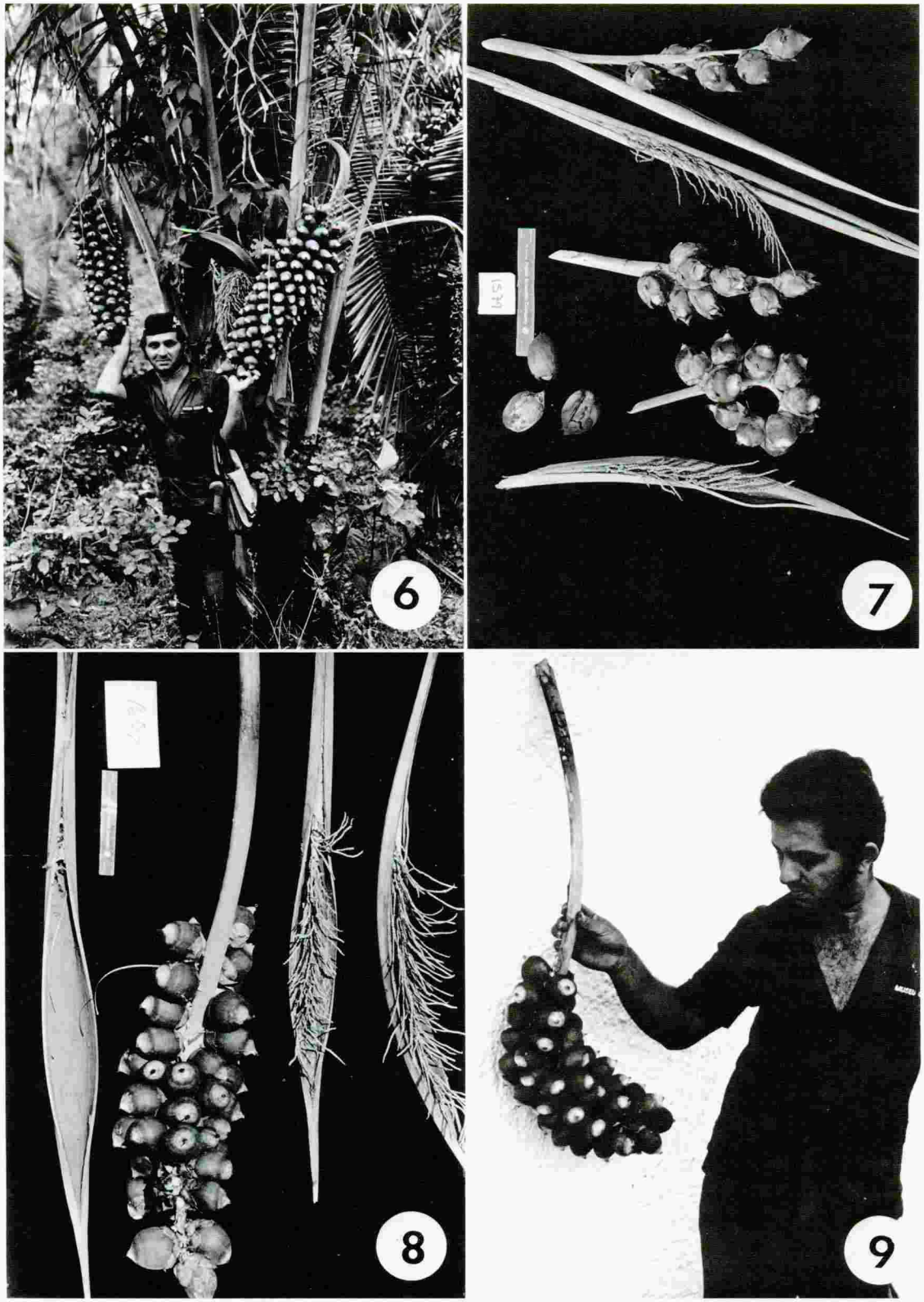


Fig. 6–9. **6.** *O. phalerata,* a young palm with 2 fruiting panicles. Note fruits deposited in spirals completely around the rachis. **7.** Fruiting panicle of *O. eichleri.* Note fruits form only along one side of the rachis, and fruit expansion during development causes the rachis to curl. **8.** Fruiting panicle of *O.* ×*teixeirana* (Balick et al. 1604). Note that the fruits are not formed in a complete spiral around the rachis; one side, or at least a portion of it, is devoid of fruits. **9.** Fruiting panicle of *O.* ×*teixeirana* (Balick et al. 1312). Note curved rachis caused by absence of fruit along one section of the rachis.

et al. 1309 (CEN, IAN, INPA, MG, NY). Estado do Maranhão: Mun. São Félix de Balsas, community known as "Poço," 4 Dec 1981, *Balick et al. 1342* (CEN, IAN, INPA, MG, NY); Mun. Bom Jardim, along Rio Pindaré at Posto Indígena Carú (FUNAI Post, Guajajara Indians), 28 Aug 1983, *Balick et al. 1468* (CEN, NY), and 1 Sep 1983, *Balick et al. 1528* (CEN, NY). Estado de Mato Grosso, Mun. de Aripuanã, in seasonally flooded forest adjacent to Rio Aripuanã, 17 Mar 1977, *Anderson 288* (MG, NY). Estado de Pará: Mun. Bragança, Village of Tracuateua, Nov 1981, *Balick et al. 1301* (CEN, IAN, INPA, MG, NY); Mun. Itupiranga, 20 km downstream on Rio Tocantins from Itupiranga at Cajazeirinha, 23 Nov 1981, *Balick et al. 1304* (CEN, IAN, INPA, MG, NY); Mun. São Félix do Estado de Piauí: Xingu, on banks of Rio Fresco ca. 50 km above confluence with Rio Xingu, 7 Jul 1980, *Anderson 391* (MG, NY). Estado do Piauí 32 km S of Teresina on road to Palmeiras along Parnaiba River, at locale called "Sumaré," Dec 1981, *Balick et al. 1351* (CEN, IAN, INPA, MG, NY).

Orbignya eichleri Drude, Mart. Fl. Bras. 3: 449, t. 103. 1881. Type: Weddell 2705 (P, n.v.).

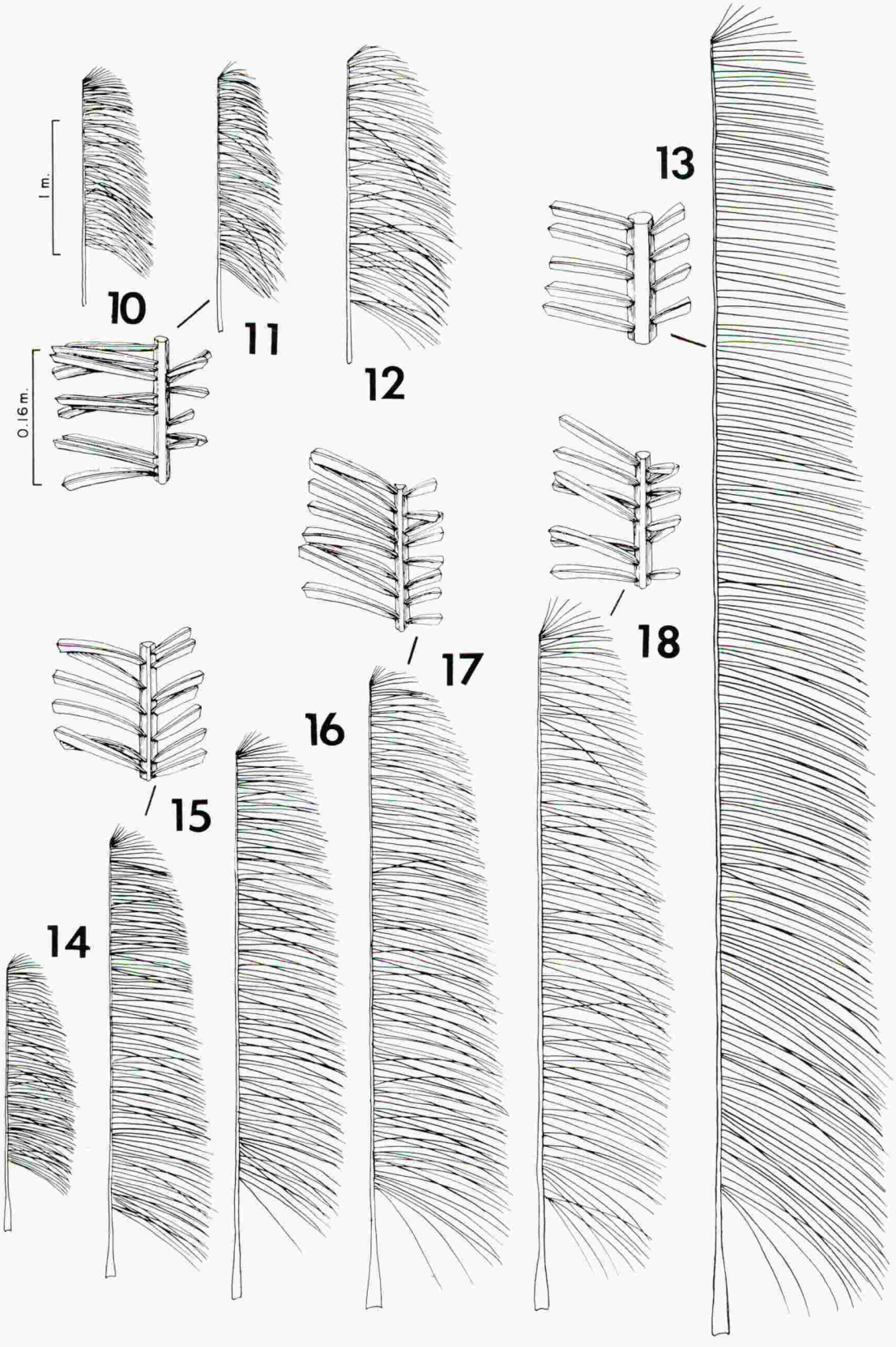
Small, solitary, stemless, pleonanthic, monoecious (or androdioecious?), palm. Leaves 3–8, spirally arranged in an erect-arching crown; sheath 20–33 cm long, thin, somewhat coriaceous, abaxial surface green, lacking striations, adaxial surface brown; petiole 30–80 cm long, ca. 1.5–2.3 cm wide, green, smooth, slightly channeled adaxially, flat to convex abaxially; rachis 1.2–2.3 m long, base trough-shaped in cross section, more or less triangular in cross section at center and toward apex, abaxial surface smooth; pinnae 76–89 per side, irregularly inserted along the rachis in groups of 2–3(–7) per side, crispate, linear-lanceolate at center of rachis, weakly plicate, acute, basally reflexed at attachment, 1-ribbed with prominent intermediate veins, dull green and smooth adaxially, green and mostly smooth abaxially, basal pinnae 45–70 cm long and 0.7–1.5 cm wide, middle pinnae 37–81 cm long and 1.4–3.0 cm wide, apical pinnae 14–42 cm long and 0.2–0.8 cm wide.

Inflorescences interfoliar, cream-white in bud, yellow at anthesis, branched to 1 order, bearing a small fibrous prophyll ca. 20 cm long; peduncular bract 35–65 cm long, coriaceous, longitudinally weakly to moderately ribbed, brown, swollen in middle, opening lengthwise, persistent, with acumen 3–12 cm long, interior surface of bract reddish brown, whitish at anthesis, becoming rust brown over time; peduncle 5–37 cm long, elliptic to ovate in cross section; rachis 17–35 cm long, strongly recurved; rachillae of staminate inflorescence 17–35 in number, 2.3–15 cm long, linear to slightly undulate, slender, attenuate, attached to the abaxial side of the rachis only, each rachilla subtended by a bracteole 1.0–4.0 mm long and bearing 5–50 flowers on abaxial side only; rachillae of adrogynous inflorescence 10–20 in number, 0.1–1.0 cm long, much thicker than rachillae on staminate inflorescences, attached to the abaxial side of the rachis only, each rachilla subtended by a bracteole 3.0–45.0 mm long and bearing 1–2 pistillate flowers at base to middle and occasionally 1–several usually inviable staminate flowers at apex.

Flowers unisexual; staminate flowers cream-yellow, slightly fragrant, asymmetrical, subtended by 1 very small bracteole per flower, 0.4–1.5 mm long; sepals (2)3(4), free or basally connate, lanceolate to triangular or trullate, 0.4–1.7(–4.9) mm long, 0.5–2.0 mm wide, membranous to coriaceous; petals 1–2(–4), free, incurved, occasionally imbricate, more or less similar in length but always with one petal wider than the other(s), the wider (or solitary) petal is 7.1–12.4 mm long and 1.5–11.6 mm wide, ovate, obovate or elliptic, apex dentate, the narrower petal(s) 6.2–11.1 mm long and 1.5–7.2 mm wide, narrowly elliptic, acute or dentate at apex, all petals membranous to fibrous with smooth margins; stamens free, 14–18(–20); filaments slender, linear to slightly narrowed toward apex, straight to occasionally undulate, 1.0–4.5 mm long, infrequently fused; anthers irregularly shaped, spirally twisted, thecae united, longitudinally dehiscent; pollen grains adherent (?); pistillode much reduced.

→

Fig. 10–18. Variation in leaves of *O. eichleri, O. phalerata* and *O. ×teixeirana*. Leaves reconstructed from data gathered from field collections; pinnae depicted only along one side of the rachis. Enlargements of rachis sections show deposition and orientation of leaves, either regularly deposited along the rachis and in a single plane (*O. phalerata*), irregularly deposited in groups of 3–4 at various angles along the rachis (*O. eichleri*) and intermediate in pinnae deposition and orientation along the rachis (*O. ×teixeirana*). **10.** *O. eichleri* (Balick et al. 1580). **11.** *O. eichleri* (Balick et al. 1578). **12.** *O. eichleri* (Balick et al. 1579). **13.** *O. phalerata* (Balick et al. 1351). **14.** *O. ×teixeirana* (Balick et al. 1597). **15.** *O. ×teixeirana* (Balick et al. 1596). **16.** *O. ×teixeirana* (Balick et al. 1559). **17.** *O. ×teixeirana* (Balick et al. 1603). **18.** *O. ×teixeirana* (Balick et al. 1604).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Pistillate flowers cream-yellow, partially covered with a rust-colored tomentum, bracteolate; sepals 3, free, imbricate, 1.9–3.5 cm long at anthesis, variably shaped but generally triangular, coriaceous, margins smooth; petals 3(4–6), free, imbricate, 1.3–2.8 cm long at anthesis, triangular to deltate, approximately same size, coriaceous, margins smooth or weakly dentate, apex acute; staminodial cupule leaving a ring about the pistil; gynoecium syncarpous; ovary superior; carpels 6–8; stigmas 6–8, apical.

Fruits elliptic, 4.8–7.7 cm long, 3.3–4.4 cm wide; 10–50 g each (dry weight), lepidote, surface gray-white at apex, rust-brown beneath, delineated in mature fruits by a weakly defined ring left by staminodial cupule; stigmatic residue persistent; a cupule of indurate perianth enclosing the base of fruit, 3.3–4.9 cm long; epicarp ca. 1.2–2.0 mm thick, fibrous; mesocarp ca. 0.4–2.7 mm thick, mealy-dry at maturity; endocarp ca. 12.5–18.2 mm in diameter, woody and very hard; seeds 4–7 (?), ovate to elliptic, 2.3–2.7 cm long, 0.6–0.8 cm wide; endosperm white, oily, homogeneous; embryo creme-white.

Specimens examined—BRAZIL. Estado de Goiás: Mun. Tocantinópolis, ca. 20 km N of town of Tocantinópolis at Posto Indígena São José (FUNAI Reservation, Apinajé tribe), 8–10 Sep 1983, *Balick et al. 1578, 1579, 1580,* and *1597* (CEN, NY). Estado do Maranhão: Mun. Carolina, ca. 10 km N of Estreito de Goiás on Belém-Brasília Highway, 1 Dec 1981, *Balick et al. 1313* (IAN, INPA, MG, NY), and ca. 20 km N of Estreito de Goiás on Belém-Brasilia Highway, 2 Dec 1981, *Balick et al. 1315* (CEN, IAN, INPA, MG, NY); Mun. Codó, 15 km N of Teresina-Belém Highway, Fazenda "Canto da Rosa," 19 Aug 1980, *Anderson 292* and *393* (NY, MG).

Orbignya ×*teixeirana* (Bondar) Balick, Pinheiro and Anderson stat. nov.

Orbignya teixeirana Bondar, Arq. Jard. Bot. Rio de Janeiro 13: 58, fig. 5, 6-3. 1954. Type: Bondar s.n., RB-80813 (RB, n.v.).

Small to medium-sized, solitary, pleonanthic, monoecious (or androdioecious?) palm; stemless or stem 0.5–7.1 m high, 19–25 cm in diameter, brown, smooth or with some leaf sheaths persistent, obscurely ringed with leaf scars.

Leaves 10–13, fewer in young or senescent plants, spirally arranged in an erect-arching crown; sheath 4–90 cm long, 15–30 cm wide, partially clasping, split opposite the petiole, thin to thick, coriaceous, abaxial surface green, with or without striations, adaxial surface brown; petiole 21–80 cm long, 3–8 cm wide, green, smooth, channeled adaxially, convex abaxially; rachis 2.0–6.4 m long, base trough-shaped in cross section, more or less 4-sided or occasionally triangular at center, becoming triangular toward apex, abaxial surface smooth or weakly to moderately orange-brown lepidote, vestiture becoming gray with age and falling away; pinnae 104–153 per side, inserted either singly or irregularly in groups of 2–4 along the rachis and either in a single plane or in several planes, rigid when young, becoming pliant with age, linear-lanceolate at center of rachis, plicate, acute, basally reflexed at attachment, 1-ribbed with prominent intermediate veins, dull green and smooth adaxially, weakly glaucous to smooth abaxially, basal pinnae 40–185 cm long and 0.5–2.5 cm wide, middle pinnae 53–112 cm long and 2.2–4.0 cm wide, apical pinnae 14–33 cm long and 0.2–1.5 cm wide.

Inflorescences interfoliar, branched to 1 order, cream-white in bud, yellow at anthesis, bearing a small fibrous prophyll ca. 30–33 cm long; peduncular bract 85–130 cm long, coriaceous to woody, longitudinally strongly-ribbed, brown, swollen in middle, opening lengthwise, persistent, with acumen 3–20 cm long, interior surface of bract whitish at anthesis, becoming rust-brown over time; peduncle 44–88 cm long, elliptic to ovate in cross section; rachis 34–99 cm long; rachillae of staminate inflorescence 41–150 in number, 1–20 cm long, linear to slightly undulate, slender, attenuate, attached to the abaxial side of the rachis only, each rachilla subtended by a bract 0.5–7.5 mm long and bearing 10–60 staminate flowers deposited on abaxial side only; rachillae of androgynous inflorescence 20–70 in number, 0.1–2.9 cm long, much thicker than rachillae on staminate inflorescences, attached to the abaxial side of the rachis exclusively or occasionally arranged spirally from the base to the middle portion of the rachis and only on the abaxial side from the middle to the apex of rachis, each rachilla subtended by a bract 0.5–30 mm long and bearing 1–2 pistillate flowers at base to middle and 1–several usually inviable staminate flowers at apex.

Flowers unisexual, staminate flowers cream-yellow, slightly fragrant, asymmetrical, subtended by (1)2(3) small bracteoles 0.3–2.0 mm long; sepals 3, free or basally connate, lanceolate to triangular, 0.6–1.6 mm long, 0.6–1.3 mm wide, membranous to coriaceous; petals 1–2, free, incurved, occasionally imbricate, more or less similar in length but always with one petal wider than the other(s), when two or

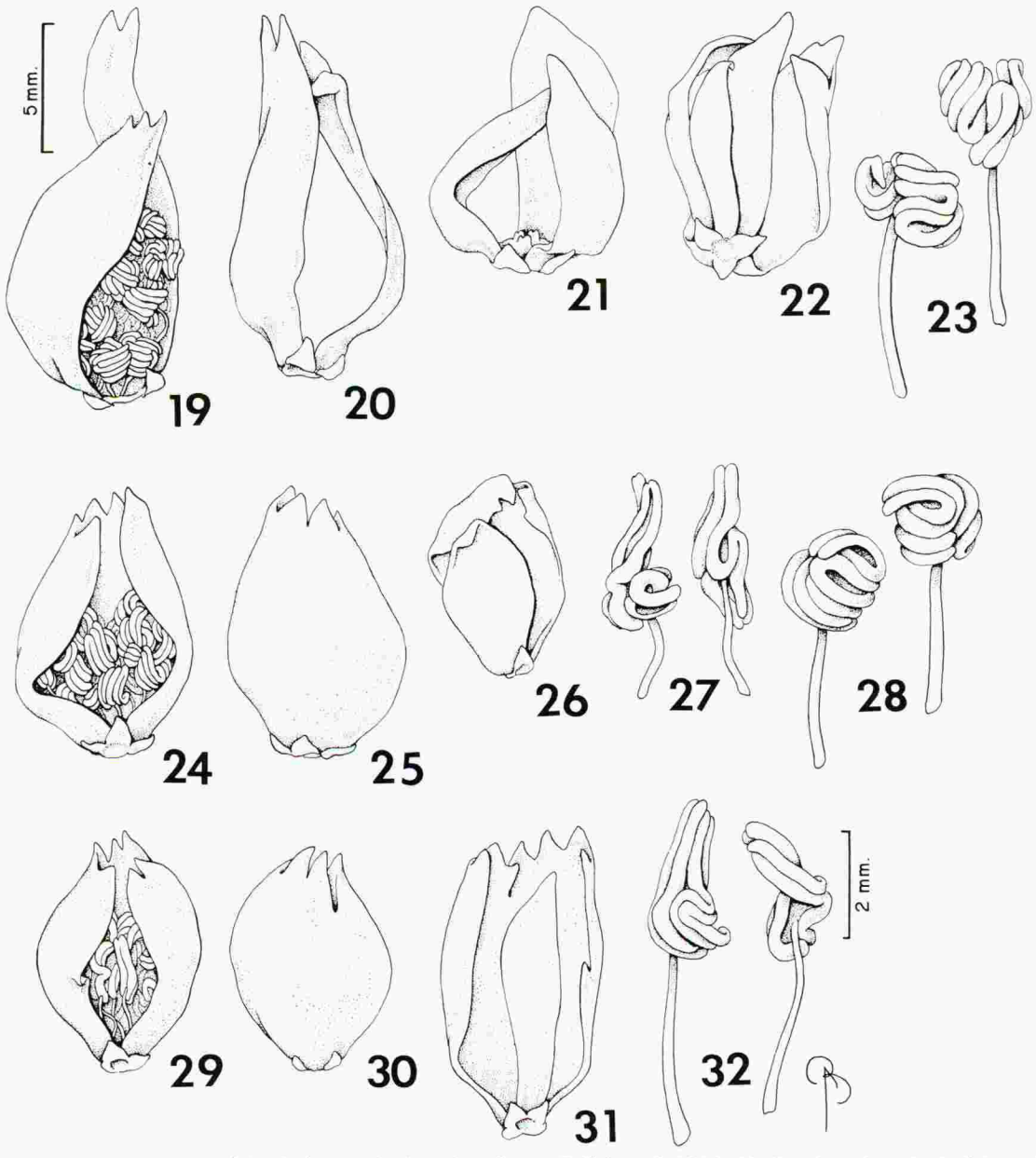
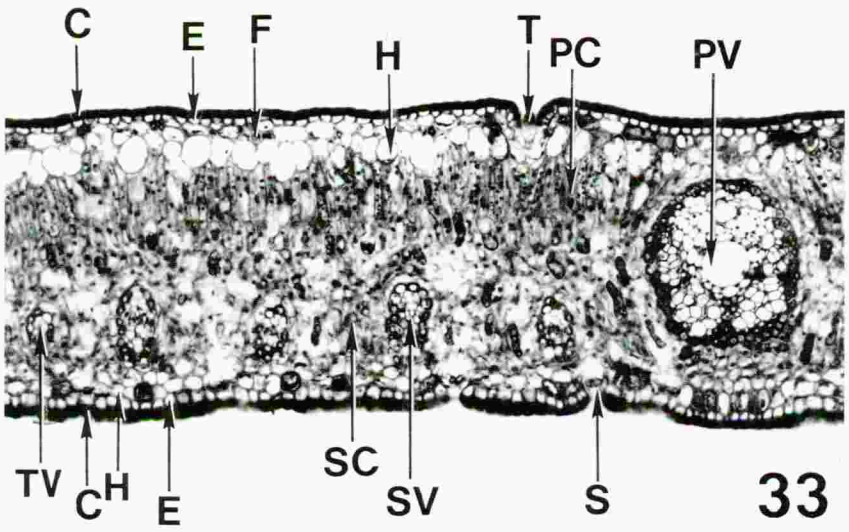


Fig. 19–23. Flowers of *O. phalerata*. **19.** Complete flower (Balick et al. 1351). **20.** Sepals and petals (Balick et al. 1351). **21.** Sepals and petals (Balick et al. 1528); note that there are three petals in this flower. **22.** Sepals and petals (Balick et al. 1354); note the rare occurrence of four petals on a single flower. **23.** Stamens with inrolled anthers (Balick et al. 1351).

Fig. 24–28. Flowers of *O.* ×*teixeirana*. **24.** Complete flower (Balick et al. 1348); note the single incurved petal. **25.** Rear view of previous figure; note incurved petal. **26.** Flower with one larger incurved petal and another smaller petal (Balick et al. 1559). **27.** Stamens with loosely inrolled anthers similar to those characteristic of *O. eichleri* (Balick et al. 1559). **28.** Stamens with tightly inrolled anthers similar to those characteristic of *O. phalerata* (Balick et al. 1348).

Fig. 29–32. Flowers of *O. eichleri*. **29.** Complete flower (Balick et al. 1597); note single petal. **30.** Rear view of previous figure. **31.** Flower with stamens removed, showing two petals (Balick et al. 1313). **32.** Stamens with loosely inrolled anthers characteristic of this species (Balick et al. 1580).

more petals present the wider petal 7.0–11.8 mm long, 4.1–6.8 mm wide, obovate or elliptic, apex dentate, the narrower petal(s) 7.0–11.5 mm long, 3.0–5.0 mm wide, narrowly elliptic to obovate, apex acute or dentate, all petals membranous; stamens free (18–)20–25(26); filaments slender, linear to slightly narrowed toward apex, straight to occasionally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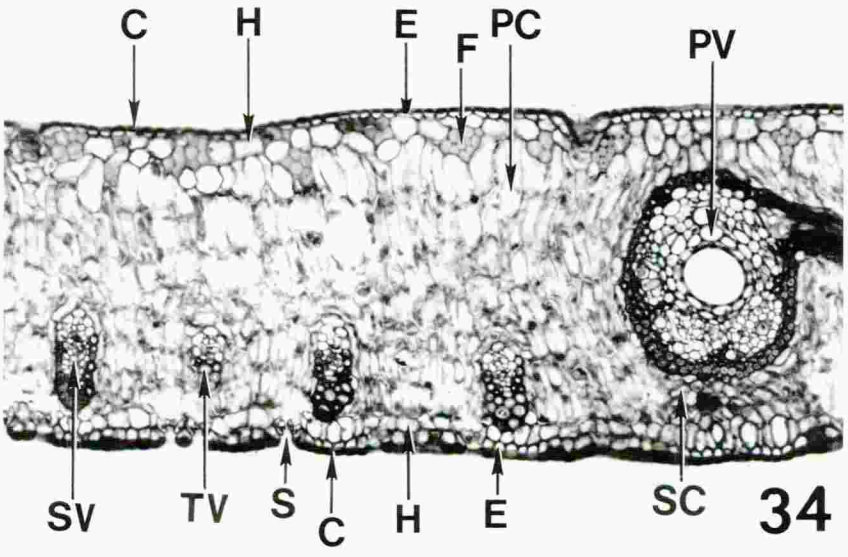
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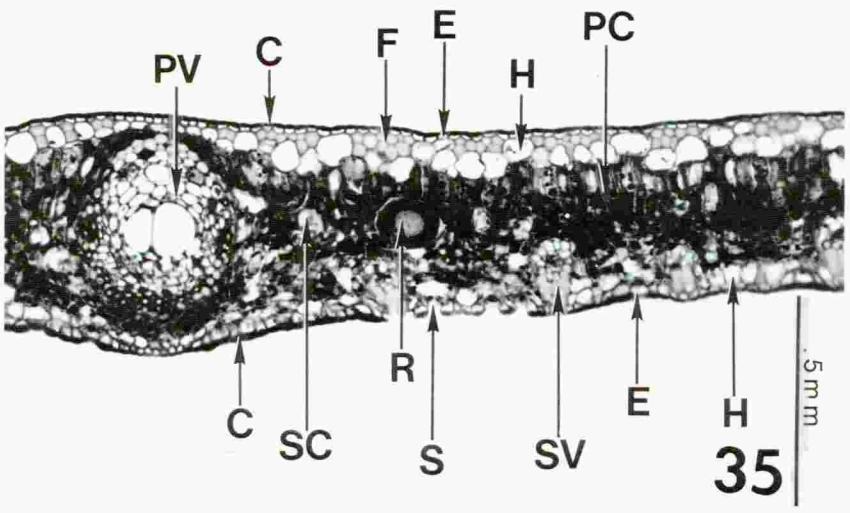
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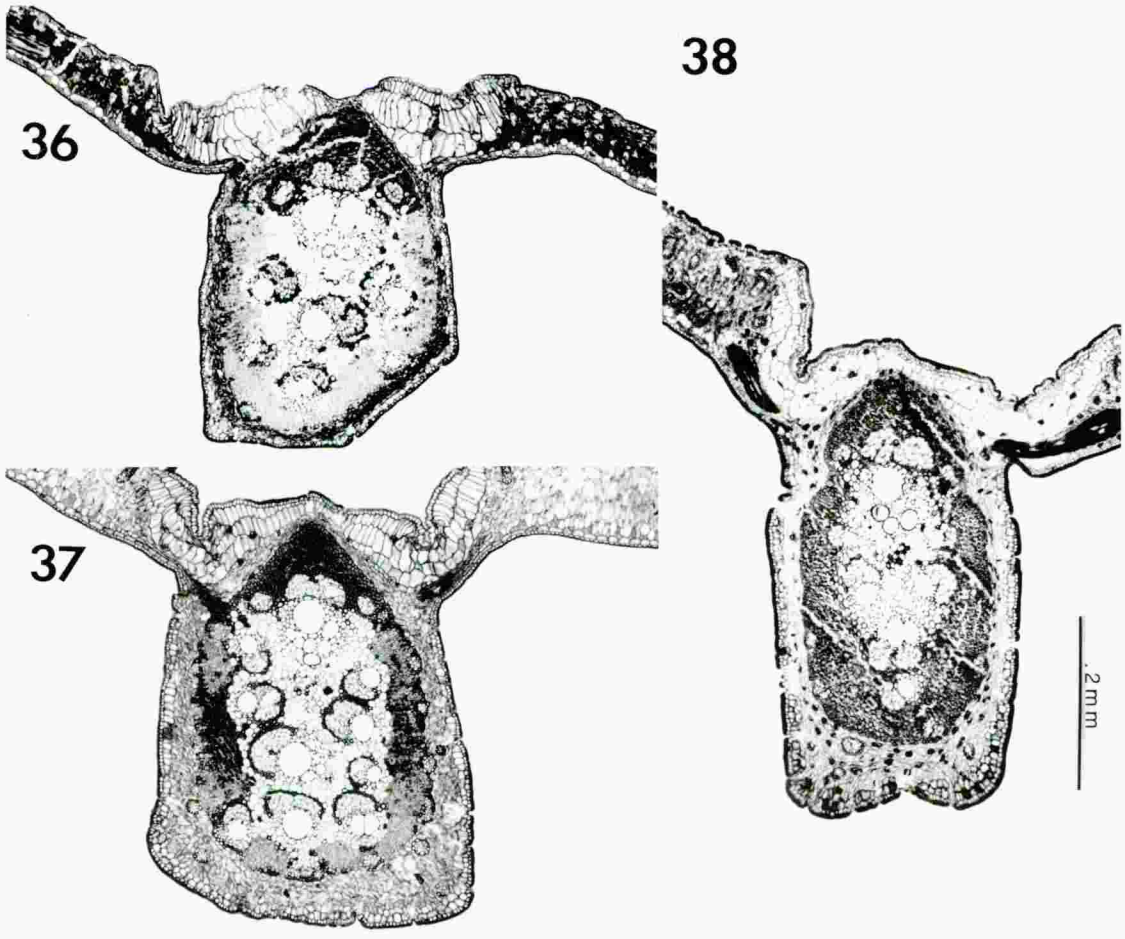

Fig. 36–38. Cross section of the leaf midrib. **36.** *O. eichleri* (Balick et al. 1313). **37.** *O.* ×*teixeirana* (Balick et al. 1347). **38.** *O. phalerata* (Balick et al. 1351).

undulate, 1.0–4.0 mm long, infrequently fused; anthers irregularly shaped, spirally twisted, roundish or elongated, thecae united, longitudinally dehiscent; pollen grains free; pistillode much reduced.

Pistillate flowers cream-yellow, partially covered with a rust-colored tomentum, bracteolate; sepals 3, free, imbricate, 2.4–3.5 cm long at anthesis, triangular to deltate, coriaceous, margins smooth; petals 3(4), free, imbricate, 2.2–3.4 cm long at anthesis, triangular to deltate, approximately the same size, coriaceous, margins smooth, apex acute or dentate; staminodial cupule leaving a ring about the pistil; gynoecium syncarpous; ovary superior; carpels 5–6; stigmas 5–6, apical.

Fruits elliptic, 5.4–9.1 cm long, 3.4–5.9 cm wide; 18–210 g each (dry weight), lepidote, surface gray-white at apex, rust-brown beneath, delineated in mature fruits by a weakly to moderately defined ring left by the staminodial cupule; stigmatic residue persistent; calyx a cupule of indurate perianth enclosing the base of fruit, 3.4–5.9 cm long; epicarp ca. 1.2–2.5 mm thick, fibrous; mesocarp ca. 3.2–5.7 mm thick, mealy-dry at maturity; endocarp ca. 18.5–30

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Fig. 33–35. Transverse section of leaves in this complex. **33.** *Orbignya phalerata* (Balick et al. 1351). **34.** *O.* ×*teixeirana* (Balick et al. 1347). **35.** *O. eichleri* (Balick et al. 1313). Legend: C = cuticle; E = epidermis; F = fibers; H = hypodermis; PC = palisade cells; PV = primary vein; R = raphide; S = stoma; SC = spongy cells; SV = secondary vein; T = trichome; TV = tertiary vein.

mm in diameter, woody and very hard; seeds 4–7, ovate to elliptic, 3.5–4.4 cm long, 1.0–1.6 cm wide; endosperm white, oily, homogeneous; embryo cream-white.

Specimens examined—BRAZIL. Estado de Goiás: Mun. Tocantinópolis, ca. 20 km W of town of Tocantinópolis at Posto Indígena São José (FUNAI Reservation, Apinajé tribe) 6–10 Sep 1983, *Balick et al. 1559, 1596, 1603,* and *1604* (CEN, NY). Estado do Maranhão: Mun. Carolina, ca. 10 km N of Estreito de Goiás on Belém-Brasília Highway, 1 Dec 1983, *Balick et al. 1312* (CEN, IAN, INPA, MG, NY); Mun. Codó, 15 km N of Teresina-Belém Highway, Fazenda "Canto da Rosa," 20 Aug 1980, *Anderson 395* and *396* (NY, MG); Mun. São Félix de Balsas, community known as "Poço," 4 Dec 1981, *Balick et al. 1347* and *1348* (CEN, IAN, INPA, NY, MG).

Descriptions of Leaf Anatomy: Orbignya phalerata Mart.—*Trichomes* present on both surfaces, clavate, irregularly distributed, sunken, 0.035–0.055 mm long, more frequent on abaxial surface and also present on midrib. *Adaxial cuticle* ca. 0.007 mm thick; *abaxial cuticle* 0.005–0.015 mm thick. *Adaxial epidermis* one layer of rectangular cells, approximately equal, longitudinally oriented, walls undulate; *abaxial epidermis* also one layer of cells with alternate narrow bands of costal cells and wider bands of intercostal cells; costal cells approximately rectangular, narrow, longer than wide and longitudinally oriented, walls undulate; intercostal cells variable in shape and size, wider than long, walls slightly undulate and closely appressed. *Stomata* present abaxially only, irregularly distributed, not in definite rows, occurring among the intercostal cells, very rarely among the costal cells; guard cells sunken, 0.017–0.025 mm deep; subsidiary cells 6, comprising a pair of terminal cells and two pairs of lateral cells (inner pair sunken and outer pair superficial); terminal cells variable in shape but predominantly tetragonal. *Adaxial hypodermis* of two layers of cells, the upper layer of smaller cells than the lower, variable but usually rounded; *abaxial hypodermis* of one layer of cells of approximately same size and shape, but more elongated in the area of the base of trichomes and stomata. *Chlorenchyma* with two layers of palisade cells, abundantly tanniniferous; spongy mesophyll of several layers of closely appressed and variably shaped cells. *Fibers* near the adaxial surface longitudinally oriented, in strands or rows, but the strands more frequent, occurring below the epidermis or below the hypodermis (1)2–4 (–14) fibers per strand or row; fibers near the abaxial surface less frequent, isolated or in small strands of 2–3, above the epidermis and/or hypodermis. *Primary veins* located in the middle portion of the mesophyll, with an outer sheath incomplete abaxially and an inner fibrous sheath completely surrounding the veins; *secondary and tertiary veins* occurring in the spongy mesophyll, always above the hypodermal layer, buttresses lacking; the outer sheaths of secondary and tertiary veins also incomplete abaxially; the inner fibrous sheath completely surrounding the veins; fibers larger in the abaxial part of the sheath. *Midrib* approximately rectangular in cross section, elevated or raised adaxially, sclerotic sheath single, pointed abaxially, with 4–8 large vascular bundles and 6–7 small vascular bundles in the periphery of the sclerotic sheath and 3–7 among the central parenchyma cells; trichomes and stomata reduced in number; some strands of fibers among the parenchyma cells (2–20 fibers per strand); structure of midrib: epidermis (1 layer of very small cells), hypodermis (2 layers of cells varying in shape at different points of midrib), and centrally closely appressed parenchyma cells. *Expansion cells* present on both sides of midrib, with three layers on each side, these layers confluent or not below sclerotic sheath. *Silica bodies* spherical-spinulose, in the lamina. Specimens examined: *Balick et al. 1301, 1342,* and *1351.*

Orbignya eichleri Drude—*Trichomes* present on both surfaces, clavate, irregularly distributed, sunken, 0.025–0.042 mm long, more frequent on abaxial surface and also present on midrib. *Adaxial cuticle* ca. 0.005 mm thick; *abaxial cuticle* 0.002–0.007 mm thick. *Adaxial epidermis* of one layer of longitudinally oriented rectangular cells, walls undulate, approximately equal; *abaxial epidermis* also of only one layer of cells with alternate bands of costal cells (narrower bands) and intercostal cells (wider bands); costal cells approximately rectangular, narrower than wide and longitudinally oriented, walls undulate; small intercostal cells, wider than long, variable in shape and size, walls undulate. *Stomata* present abaxially only, rarely among the costal cells; guard cells sunken, 0.012–0.022 mm deep; subsidiary cells 6, comprising a pair of terminal cells and two pairs of lateral cells (inner pair sunken and outer pair superficial); terminal cells variable in shape but mostly triangular; adjacent terminal cells frequently fused. *Adaxial hypodermis* of one layer of cells, longitudinally oriented and approximately same shape; *abaxial hypodermis* of one layer of cells, variably shaped, longitudinally oriented, a little smaller

than the cells of adaxial surface, more elongated near the area of the bases of trichomes and stomata; abaxial layer of hypodermal cells always interrupted by the buttresses of the secondary and tertiary veins, the lower portions of the veins touching the abaxial epidermis. *Chlorenchyma* with 1–2 layers of palisade cells, abundantly tanniniferous; spongy mesophyll of several layers of closely appressed variably shaped cells. *Fibers* near the adaxial surface longitudinally oriented, in massive groups, regularly distributed, occurring below the epidermis, (1–)6–7(–22) fibers per strand; fibers near the abaxial surface less frequent, isolated or in small strands of 2–3, above the epidermis and/or hypodermis. *Primary veins* located in the middle portion of the mesophyll, independent of both surfaces, with an outer sheath incomplete abaxially and an inner fibrous sheath completely surrounding the veins; *secondary and tertiary veins* occurring in the spongy mesophyll extending through the hypodermal layer and touching the epidermis in well characterized and very frequent buttresses; an inner fibrous sheath of the secondary and tertiary veins present, the extended cells incomplete in their lower portions and the inner fibrous sheaths incomplete in their upper portions and not completely surrounding the veins; fibers larger in the abaxial part of the sheath. *Midrib* approximately square in cross section, elevated or raised adaxially, sclerotic sheath single, pointed abaxially, with 5 large vascular bundles and 1–4 smaller vascular bundles; 0–10 small vascular bundles in the periphery of the sclerotic sheath and 0–3 among the parenchyma cells; trichomes and stomata present; some strands of fibers in the upper portion of midrib, among the parenchyma cells and hypodermal cells (1–9 fibers per strand); structure of midrib: epidermis (1 layer of very small cells), hypodermis (2 layers of cells) and closely appressed parenchyma cells; *Expansion cells* present in layers on each side of midrib with 3 layers per side, these layers confluent or not below the sclerotic sheath. *Silica bodies* spherical-spinulose in the lamina. Specimens examined: *Balick et al. 1313, 1316,* and *1317.*

Orbignya ×*teixeirana* (Bond.) Balick, Pinheiro and Anderson—*Trichomes* on both surfaces, more frequent on abaxial surface, clavate, irregularly distributed, sunken, 0.040–0.047 mm long, present on midrib. *Adaxial cuticle* 0.005–0.007 mm thick; *abaxial cuticle* ca. 0.007 mm thick. *Adaxial epidermis* one layer of rectangular cells, walls undulate, approximately equal, longitudinally orientated, rather uniform; *abaxial epidermis* also of one layer of cells with alternate bands of costal cells (narrower bands) and intercostal cells (wider bands); costal cells rectangular, longitudinally oriented, walls undulate; intercostal cells closely appressed, variable but usually rounded. *Stomata* present abaxially only, irregularly distributed, not in definite rows, occurring among the intercostal cells and very rarely among the costal cells; guard cells sunken, 0.012–0.020 mm deep; subsidiary cells 6, comprising a pair of terminal cells and two pairs of lateral cells (inner pair sunken and outer pair superficial); terminal cells variable in shape but predominantly tetragonal. *Adaxial hypodermis* 1(–2) layer(s) of rounded cells; adaxially fibers replacing most cells of the outer layer of hypodermis; *abaxial hypodermis* a single layer of cells, longitudinally oriented, a little smaller than the cells of the adaxial hypodermis, more elongated near the base of the trichomes and stomata; the abaxial layer of hypodermal cells almost completely continuous but occasionally interrupted by the lower portions of secondary and tertiary veins. *Chlorenchyma* with 1–2 layers of palisade cells, spongy mesophyll of several layers of closely appressed and variably shaped, abundantly tanniniferous cells. *Fibers* near the adaxial surface occurring in longitudinally oriented, moderate strands and less frequently in rows; (1–)6–8(–14) fibers per strand; fibers near the abaxial surface less frequent, isolated or in small bundles of 1–4 in the spongy mesophyll. *Primary veins* in the middle portion of the mesophyll, independent of both surfaces, with an outer sheath incomplete abaxially and an inner fibrous sheath completely surrounding the veins; *secondary and tertiary veins* occurring in the spongy mesophyll; the lower portion of the secondary and tertiary veins extending part way through the hypodermis but only rarely touching the epidermis and forming buttresses; the outer sheath of the secondary and tertiary veins of extended cells incomplete in the lower portion of the veins, the inner sheath well developed in the lower portion but incomplete in the upper portion and not completely surrounding the veins; fibers larger in the abaxial part of the sheath. *Midrib* approximately square in cross section, elevated or raised adaxially, sclerotic sheath single, pointed abaxially with 2–3 large vascular bundles and 3–4 smaller vascular bundles; 5–12 small vascular bundles in the periphery of the sclerotic sheath and 2–4 among the parenchyma cells; trichomes and stomata on the midrib; some strands of fibers among the parenchyma cells (1–7 fibers per strand); structure of midrib: epidermis (1 layer of very small

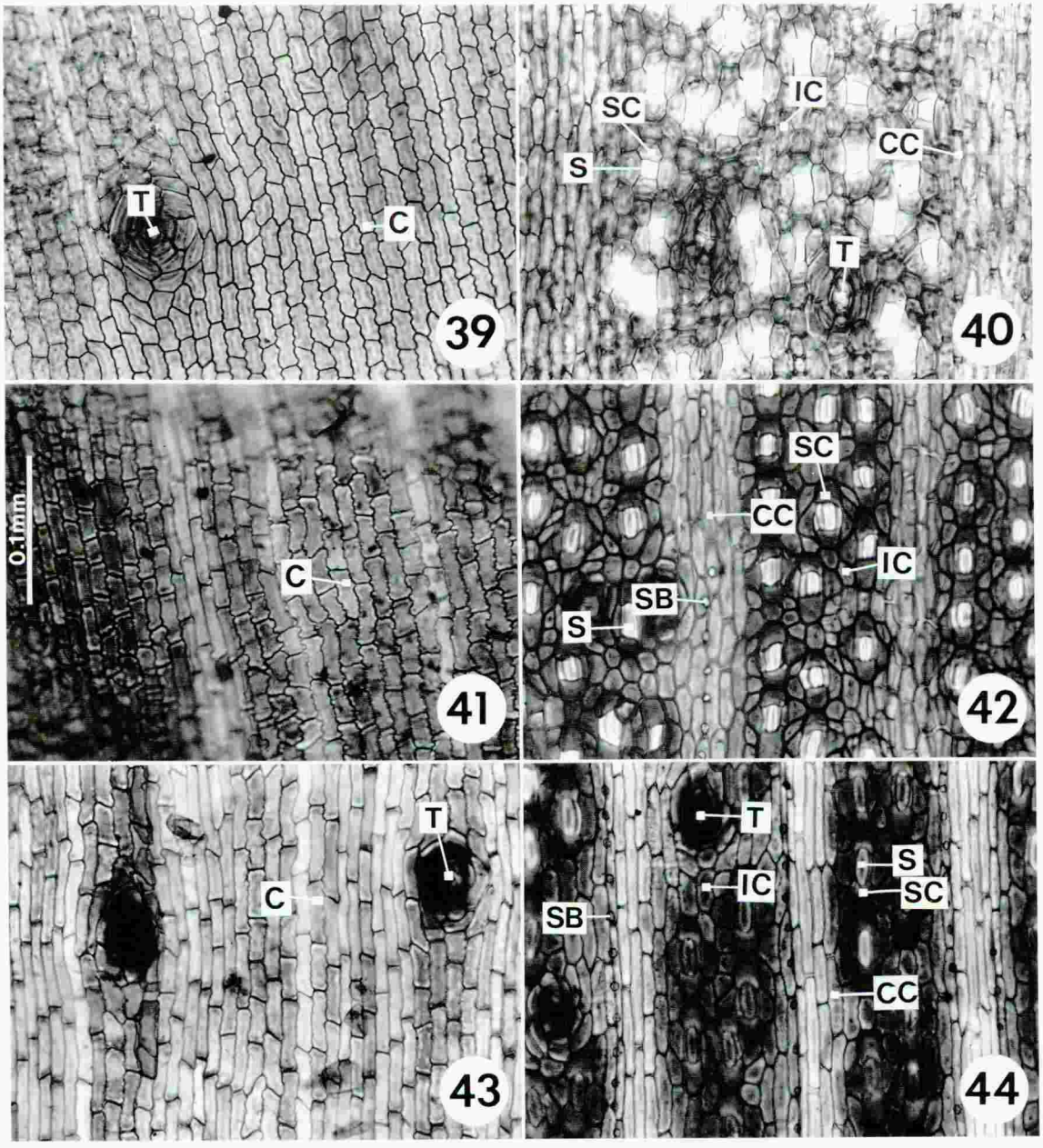

Fig. 39–44. Epidermal peels. **39.** *Orbignya phalerata* (Balick et al. 1351), adaxial epidermis. **40.** *O. phalerata* (Balick et al. 1351), abaxial epidermis. **41.** *O. ×teixeirana* (Balick et al. 1347), adaxial epidermis. **42.** *O. ×teixeirana* (Balick et al. 1347), abaxial epidermis. **43.** *O. eichleri* (Balick et al. 1313), adaxial epidermis. **44.** *O. eichleri* (Balick et al. 1313), abaxial epidermis. Legend: C = adaxial cells; CC = costal cells; IC = intercostal cells; S = stomata; SB = silica bodies; SC = subsidiary cells; T = trichomes.

cells), hypodermis (2 layers in the upper portion and 1 layer in the remaining portion of midrib) and closely appressed parenchyma cells. *Expansion cells* present in layers on each side of midrib (3–4 layers per side), the layers confluent or not below the sclerotic sheath; sometimes some expansion tissue in the margins of pinnae. *Silica bodies* spherical-spinu-

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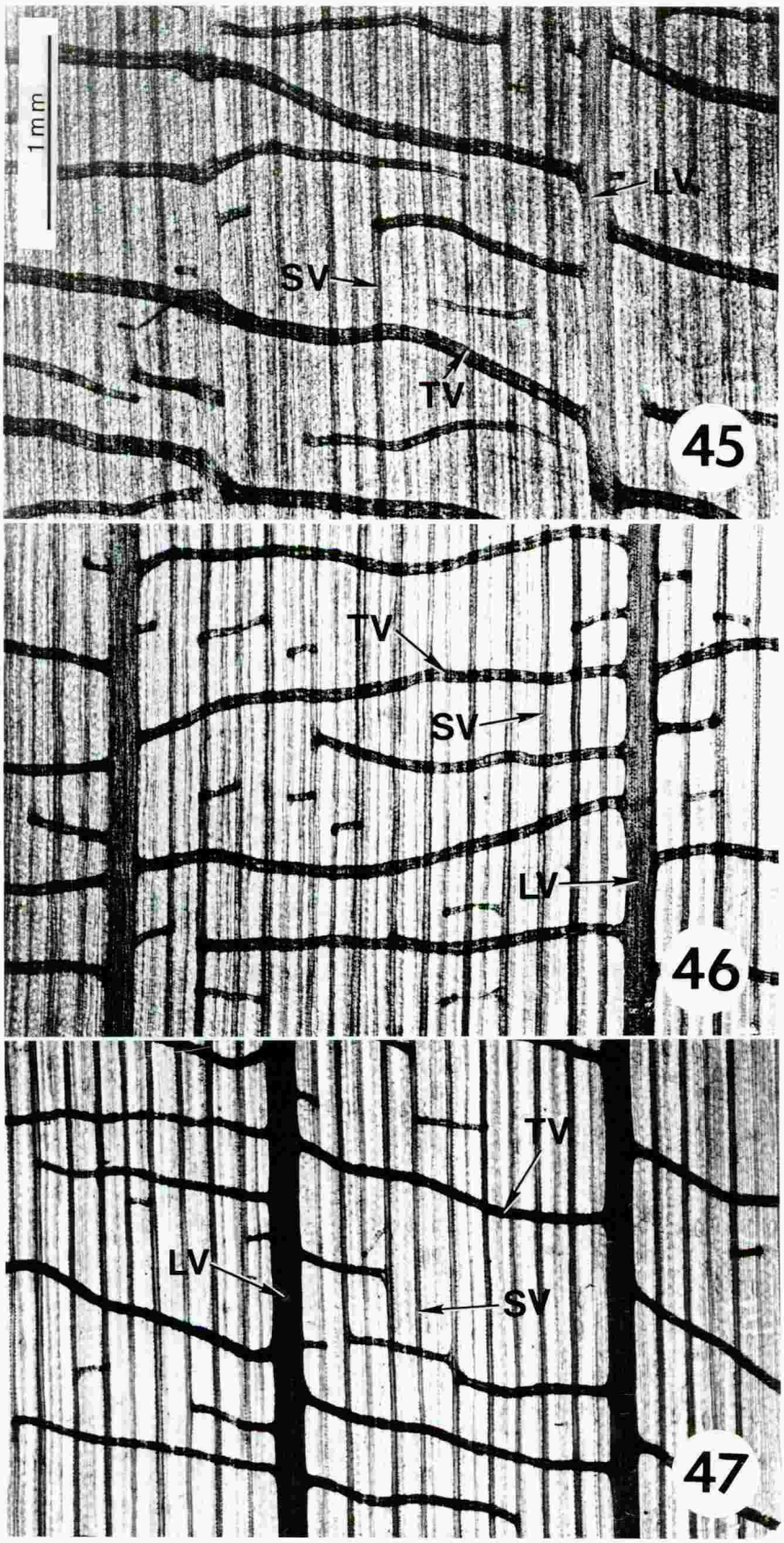
Fig. 45–47. Leaf clearings showing venation. **45.** *O. phalerata* (Balick et al. 1351). **46.** *O. ×teixeirana* (Balick et al. 1347). **47.** *O. eichleri* (Balick et al. 1313). Legend: LV = large vein; SV = small vein; TV = transverse vein.


1 mm
LV
SV
TV
45
TV
SV
LV
46
TV
LV
SV
47

lose in the lamina. Specimens examined: *Balick et al. 1312, 1347*, and *1348*.

DISCUSSION—As shown in Tables 1 and 2 and Fig. 2–9, a wide variety of quantitative and qualitative characters are intermediate in the purported hybrid. These intermediate characters range from morphology (e.g., stem length, leaf size, and structure of the flower) to anatomical features (e.g., thickness of abaxial hypodermis and presence of buttresses). In addition to the morphological and anatomical evidence, field observations revealed that the hybrid is apparently limited to areas where both *Orbignya phalerata* and *O. eichleri* occur (Fig. 1), thus providing further support for its hybrid status. Based on these considerations, we conclude that what was formerly known as *Orbignya teixeirana* Bondar is, in fact, a natural hybrid arising from the crossing of babassu, *O. phalerata* Mart., and piassava, *O. eichleri* Drude. We thus propose that the scientific name of the perinão palm be changed to *Orbignya* ×*teixeirana* (Bondar) Balick, Pinheiro & Anderson. Within the natural populations of *Orbignya* ×*teixeirana,* a great range of variation can be found, as is evident from Table 1. This variation has been studied in a population located in the basin of the Parnaíba and Itapecuru rivers of Maranhão and Piauí States, Brazil (Medeiros-Costa, de Campos Mendes, and de Castro Brito, 1985). On the basis of this study, three morphotypes were recognized, all intermediate in morphology between the two parent species. Recognition of these morphotypes was based on measurements of the rachis, number of pinnae, number and percentage of grouped and regular pinnae, percentage of rachis with regular pinnae and number of stamens in the flower. This exhaustive study of a single population provides further evidence that *Orbignya* ×*teixeirana* comprises a highly variable hybrid swarm intermediate in size and structure between the parents. In future publications we shall propose hybrid status for other taxa in the babassu complex, based on various lines of evidence. The results of our research in this complex have convinced us that some proportion of the pronounced morphological variability in palms, especially in the subtribe Attaleinae (Dransfield and Uhl, 1986), can be attributed to their propensity to hybridize freely in the wild. The complexities of hybridization in palms will ensure decades of research problems for palm taxonomists, at least as long as native palm habitats remain intact. The current trend toward resolution of taxonomic questions in palms through extensive field work (Tomlinson, 1979) will produce an increased understanding of the extent of hybridization in some elements of the family, and, we feel, a considerable reduction in the number of valid taxa at the specific level within those groups where hybridization can be identified.

LITERATURE CITED

ANDERSON, A. B., AND M. J. BALICK. In press. Taxonomy of the babassu palm complex. Syst. Bot.

BALICK, M. J., A. B. ANDERSON, AND M. F. DA SILVA. 1982. Palm taxonomy in Brazilian Amazonia: an evaluation of the state of systematic collections in regional herbaria. Brittonia 34(4): 463–477.

BONDAR, G. 1954. Nova espécie de *Orbignya,* produtora do óleo de babaçu. Arch. Jard. Bot. Rio de Janeiro. 13: 57–59.

DAHLGREN, B. E., AND S. F. GLASSMAN. 1963. A revision of the genus *Copernicia* II. West Indian species. Gentes Herb. 9: 43–232.

DRANSFIELD, J., AND N. W. UHL. 1986. An outline of a classification of palms. Principes 30(1): 3–11.

GLASSMAN, S. F. 1968. Studies in the palm genus *Syagrus* Mart. Fieldiana, Bot. 31(17): 363–397.

———. 1970. A new hybrid in the palm genus *Syagrus* Mart. Fieldiana, Bot. 32(16): 241–257.

———. 1971. A new palm hybrid from the Fairchild Tropical Garden. Principes 15(3): 79–88.

———. 1972. Systematic studies in the leaf anatomy of palm genus *Syagrus*. Amer. J. Bot. 59(8): 775–788.

———. 1977. Preliminary taxonomic studies in the palm genus *Orbignya* Mart. Phytologia 36: 89–115.

MARKLEY, K. S. 1971. The babassu oil palm of Brazil. Econ. Bot. 25(3): 267–304.

MARTENS, J., AND N. W. UHL. 1984. Methods for the study of leaf anatomy in palms. Stain Technol. SS(4): 241–246.

MEDEIROS-COSTA, J. T., A. M. DE CAMPOS MENDES, AND J. L. DE CASTRO BRITO. 1985. Morfodiagnose de *Orbignya teixeirana* Bondar (Palmae-Cocosoideae) nos estados do Piauí e Maranhão. Pesquisa em Andamento (EMBRAPA/UEPAE de Teresina) No. 39: 1–5. Offset.

O'BRIEN, T. P., AND M. E. MCCULLY. 1981. The study of plant structure, principles and selected methods. Termarcarphi PTY. Ltd., Melbourne.

PICK, P. J., J. M. FRAZÃO, W. P. MASON, P. H. MAY, AND W. MILFONT, JR. 1985. Babassu (*Orbignya* species): Gradual disappearance vs. slow metamorphosis to integrated agribusiness. A report prepared for the New York Botanical Garden Institute of Economic Botany. January.

READ, R. W. 1975. The genus *Thrinax* (Palmae: Coryphoideae). Smithson. Contrib. Bot. 19: 1–98.

TOMLINSON, P. B. 1961. Anatomy of the Monocotyledons II. Palmae. Oxford University Press, London.

———. 1979. Systematics and ecology of the Palmae. Annual Review of Ecology and Systematics 10: 85–107.

UHL, N. W. 1972. Leaf anatomy in the *Chelyocarpus* alliance. Principes 16(3): 101–110.

———. 1978. Leaf anatomy in the species of *Hyophorbe* (Palmae). Gentes Herb. 11: 268–283.

WESSELS BOER, G. 1971. *Bactris* × *moorei,* a hybrid in palms. Acta Bot. Neerl. 20(1): 167–172.